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Test of Ecogeographical Rules on Sparrows (*Passer* spp.) along the Elevation Gradient of the Himalaya in Central Nepal

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Abstract: Animals inhabiting colder climates have a larger body size (Bergmann's rule) and smaller body extremities (Allen's rule), which help homeothermic animals to retain heat. Such ecogeographical phenomena have frequently been observed in animals along the latitudinal gradient and have occasionally been tested along the elevational gradient. This study tested whether these ecogeographic rules hold true for the morphology of sparrows (*Passer* spp.) along the elevational gradient offered by the Himalaya in central Nepal. Seventy house sparrows and twenty-eight tree sparrows were captured from 22 different localities of central Nepal between 100 and 3400 m asl, and morphological traits such as body size (body mass, tarsus length, wing length and tail length) and body extremities (bill length and bill width) were measured. Linear regression analysis was used to test the association of morphological measurements with elevation and climatic variables. House sparrows (*Passer domesticus*) had a wider elevational distribution range and exhibited significantly larger body sizes than the Eurasian tree sparrows (*P. montanus*). House sparrows had larger body sizes and smaller bills at higher elevations in adherence to Bergmann's rule and Allen's rule. Bill length in house sparrows showed a positive association with the temperature following the proposition of Allen's rule. However, the morphological measurements in Eurasian tree sparrows did not show a distinct pattern with elevation and climatic variables. Therefore, this study concludes that ecogeographical phenomena such as Bergmann's rule and Allen's rule could be species-specific based on their biological and ecological characteristics.

Keywords: Allen's rule; Bergmann's rule; central Himalaya; eco-geography; morphometrics

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1. Introduction

Ecological traits such as body size vary widely within and among animal species with changes in environmental selective forces [1]. Temperature is one of the abiotic factors that has an important influence on the evolution of body size [2]. Based on the relationship between temperature and body size, two long-standing eco-geographical rules have been postulated: Bergmann's rule [3] and Allen's rule [4].

According to Bergmann's rule, larger endothermic animals are found in a colder climate, and smaller endothermic animals in a warmer climate, for thermoregulatory reasons [3,5]). Larger animals can better endure cold temperatures because the larger the animal is, it has to produce less heat in relation to its size to raise the internal temperature above its surrounding [6]. However, smaller animals are found in a warmer climate, because the smaller the animal, the greater its surface area to volume ratio and more heat is dissipated from the body [5]. Allen's rule also explains the diversity of structure among species based on temperature. It states that the relative size of the body extremities such as limbs, tails, ears and bills in endothermic species, are smaller in a colder environment in order to reduce thermoregulatory costs. Such a pattern is observed more frequently in birds than in mammals [4].

Although Bergmann's rule and Allen's rule were originally proposed for the latitudinal gradient, they have been tested for elevational gradients as well. Empirical studies have found Bergmann's and Allen's rule predicted morphological patterns in numerous mammals [7,8] and birds [7,9–12]. However, species not following the pattern or showing the opposite pattern have also being reported [13–15]. Among the birds studied, Passerines such as *Cinclus cinclus* [16], *Cyanistes caeruleus* [17], and *Suiriri suiriri* [18] did not follow distinct body size patterns with temperature. The Central Himalaya, with a huge elevational gradient from 60 m (m) to 8848 m above sea level (m asl) within about 200 km (km) of north–south span [19], provide unique opportunities to assess the ecological rules explaining the distribution and morphological variations among the animals. Ecogeographical rules such as Bergmann's rule and Allen's rule have not yet been tested on the Himalayan avian fauna.

The house sparrow (*Passer domesticus*) and Eurasian tree sparrow (*P. montanus)* are traditionally associated with human habitation and are known for their occurrence within human settlements [20]. However, due to urbanization and changes in the landscape, their population is decreasing [21]. Sparrows have a wide range of distribution in Nepal [22] but scientific assessments on them are still scant. Therefore, they could be the best avian representatives to assess the impacts of elevational gradients in their distribution and morphological variations. Hence, this study aimed to test the compliance of *Passer* spp. to Bergmann's and Allen's hypotheses by morphometric measurements along the elevational gradient in central Nepal. Furthermore, it examined the association between morphological variation in sparrows and climatic variables.

2. Materials and Methods

2.1. Study Area

Central Nepal extends from 26°43′51′′ to 28°23′46′′ N latitude and 85°54′35′′ to 86°01′18′′ E longitude (Figure 1). The north–south stretch of central Nepal is divisible into five physiographic regions namely; Terai (60 to 130 m asl), Siwaliks (130 to 1200 m asl), Middle Mountains (1200 to 3300 m asl.), High Mountains (3300 to 4000 m asl) and High Himalaya (4000 to 8848 m asl) [23].

The climate is diverse, ranging from tropical to alpine type. The Terai is tropical, and Siwalik is subtropical. Middle mountains are subtropical in valley bottoms, warm temperate on the valley side and cool temperate on higher ridges. The high mountains and the high Himalayas are alpine with nival zones above the snowline [23]. The Terai and Siwaliks are characterized by Savana type grasslands and evergreen forests. *Shorea robusta* is the dominant tree in the forest along with *Bombax ceiba*, *Garuga pinnata*, etc. This region is the habitat of globally threatened flagship species such as *Panthera tigris*, *Elephas maximus*, and *Rhinoceros unicornis.*

The Siwaliks and middle mountains consist of subtropical deciduous hill forests that are dominated by *Shorea robusta*, *Dalbergia sissoo*, *Schima wallichii*, *Castanopsis indica*, rhododendron forests, etc. Animal species such as *Panthera pardus*, *Neofelis nebulosa*, *Macaca assamensis* etc. inhabit this region. The high mountains and Himalayas are characterized by broad-leaved forests including tree species such as *Abies spectabilis*, *Pinus wallichiana*, *Rhododendron campanulatum*, etc. The wild animals of conservation importance from the area include *Ailurus fulgens*, *Pseudois nayaur*, *Hemitragus jemlahicus*, etc. [24].

2.2. Field Survey

Field surveys were conducted in central Nepal from October 2019 to March 2021 at elevations ranging from 100 m asl (Chitwan) to 3400 m asl (Langtang National Park, Rasuwa). Data were collected opportunistically at 22 specific sampling sites distributed across several districts of central Nepal including Chitwan, Makawanpur, Kavrepalanchok, Kathmandu, Bhaktapur, Rasuwa and Nuwakot (Figure 1).

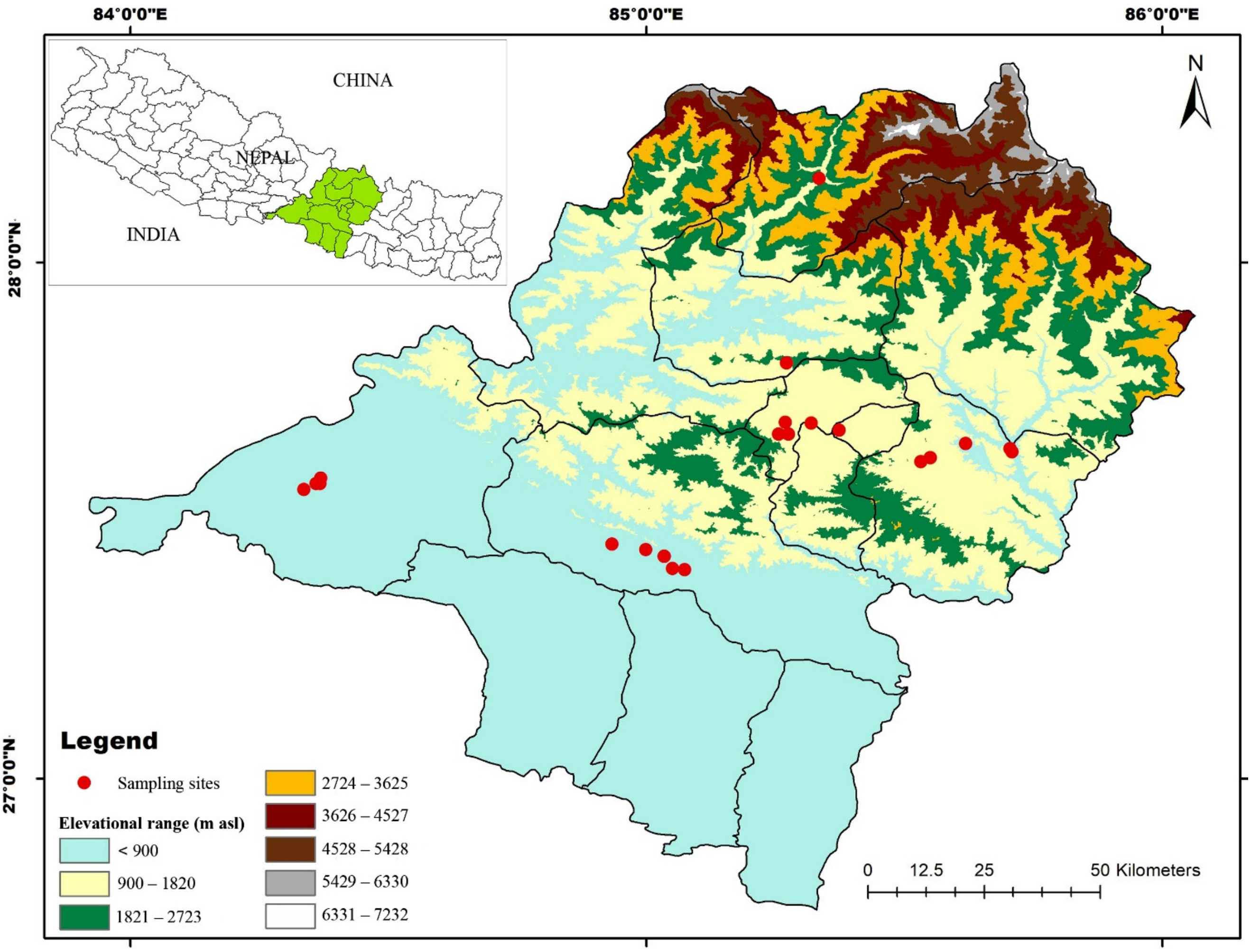

Figure 1. Map of central Nepal showing sampling areas (red dots) of *Passer* spp. from different elevations.

Upon encountering a flock of *Passer* spp., GPS points were recorded using Garmin eTrex 10; flock size was estimated, and sex was categorized. For flock size determination, the fixed-radius point count method was followed [25]. The number of birds in each flock was counted that arrived at the study site during the first five minutes of observation. Given the birds' mobility and difficulty in individual recognition, counting during the first five minutes of observation was done to help reduce the likelihood of recounting the same individual.

Birds were observed at a distance of approximately 20 m using the Vixen binoculars with 10 × 42 magnification. For identification and sex determination of *Passer* spp., the field book 'Birds of Nepal' [26] was used. Male house sparrows are bright in color. They have a grey head with chestnut side and nape, white cheeks and black throat upper breast, whereas female house sparrows are plain buffy-brown in color. They have pale buff supercilium, dark brown streaking on the buffish mantle and unstreaked greyish-white underparts [26]. Sex determinations (based on morphological differentiation) for individuals of Eurasian tree sparrows could not be performed.

2.3. Morphological Measurements

Following the guidelines outlined in 'Wild Bird Capture Techniques' [27], a mist net (six meters in length by three meters in width with four horizontal pockets, 15 mm mesh size and 0.08 mm monofilament) was installed at the sites where either house or Eurasian tree sparrows were observed. The movement of the study species was observed beforehand, and the mist net was fitted near their foraging or nesting site where the movement occurred most frequently. Food bait (rice grain) was also used to increase the probability of capture. Individuals were captured either in the morning (7 to 11 AM) or late afternoon (3 to 6 PM) when they were actively foraging. After the mist net was installed, the researchers moved 30 to 40 m away from the site. The net was examined frequently, and a bird was extracted as soon as it was caught in the net. During the extraction, if a bird was entangled, the net was cut to avoid injury to the bird. The extracted bird was immediately taken for morphological measurement. If multiple birds were caught at the same time, they were extracted one by one and placed in separate cloth pouches and hung in a cool, dark place until measurements of the previous bird were finished.

Morphological indices such as body mass, tarsus length, wing length, tail length, bill length and bill width of captured adult individuals were measured. All the morphological measurements were taken following procedures outlined in "Measurements of Birds" [28]. Among Passerine birds, wing length [29] or tarsus length [30] is regarded as the best predictor of body size. The tarsus length is full-grown at fledging and remains constant thereafter [29]. Hence, tarsus length and wing length of fully grown fledges were used as proxies of body size for testing the Bergmann's rule in this study.

The body mass was measured using a digital scale (accuracy of 0.01 g). Since the digital scale was flat, the bird was placed in a paper roll to facilitate measurement, with the weight of the roll deducted. Tarsus length, bill length and width were measured with digital calipers (accuracy 0.01 mm). The tarsus length was measured from the joint between the tibia and metatarsus to the distal edge of the last undivided scute on the anterior surface. Bill length was measured from the nostril. The length from the middle of the anterior end of the nostril in a straight line to the anterior end of the maxilla was taken. Bill width was measured from the base of the exposed culmen. Wing length and tail length were measured using a ruler. The measurement of wing length was taken from the farthest anterior edge of the wrist joint to the top of the longest primary feather while the wing was in a closed state. Tail length was measured from the middle of the rectrices to the longest tail feather when the tail was closed.

Once the measurements were completed, the bird was marked on the leg using a black permanent marker and released back from where they were initially captured.

2.4. Environmental Variables

Bioclimatic variables for each site were obtained from WorldClim Version 2.1 (www.worldclim.org, accessed on 21 July 2021) for 30 years (1970–2000) with 30 arc-seconds spatial resolution. Among 19 variables retrieved, annual mean temperature (bio1), temperature seasonality (bio4), the maximum temperature of the warmest month (bio5), minimum temperature of the coldest month (bio6), temperature annual range (bio7), mean temperature of warmest quarter (bio10), mean temperature of coldest quarter (bio11), annual precipitation (bio12), precipitation seasonality (bio15), precipitation of warmest quarter (bio18) and precipitation of coldest quarter (bio19) were included in the analysis following Fan et al. [14].

2.5. Data Analysis

A distribution map was created using the GPS coordinates of observed flocks of sparrows in ArcMap 10.8. The inter-species differences in morphological measurements between *P. domesticus* and *P. montanus* were tested for the statistical significance by unpaired *t*-test. The collinearity among the six morphological characters measured for sparrows was tested by using the 'ggcorrplot' package in R statistical software [31]. Those variables had a pairwise Pearson's correlation coefficient of <0.6 (Supplementary Figure S1); hence, all six morphological characters were used for downstream analysis. The effect of elevational gradients and environmental variables on the morphology of *Passer* spp. was examined using a linear regression model (elevation versus body size, elevation versus body mass, and bioclimatic variables versus morphological measurements).

3. Results

3.1. Elevational Distribution of Sparrows in Central Nepal

House sparrows were observed from 149 m asl to 1518 m asl, whereas Eurasian tree sparrows were found from 442 m asl to 1738 m asl (Figure 2). A total of 472 house sparrows were observed at 17 sampling sites with an average flock size of 28 individuals. The largest flock size recorded consisted of 59 individuals (27 females and 32 males) from Paanchkhal, Kavrepalanchok at an elevation of 860 m asl. The smallest flock size included five individuals (two females and three males) from Sangam Tole, Makwanpur at 448 m asl.

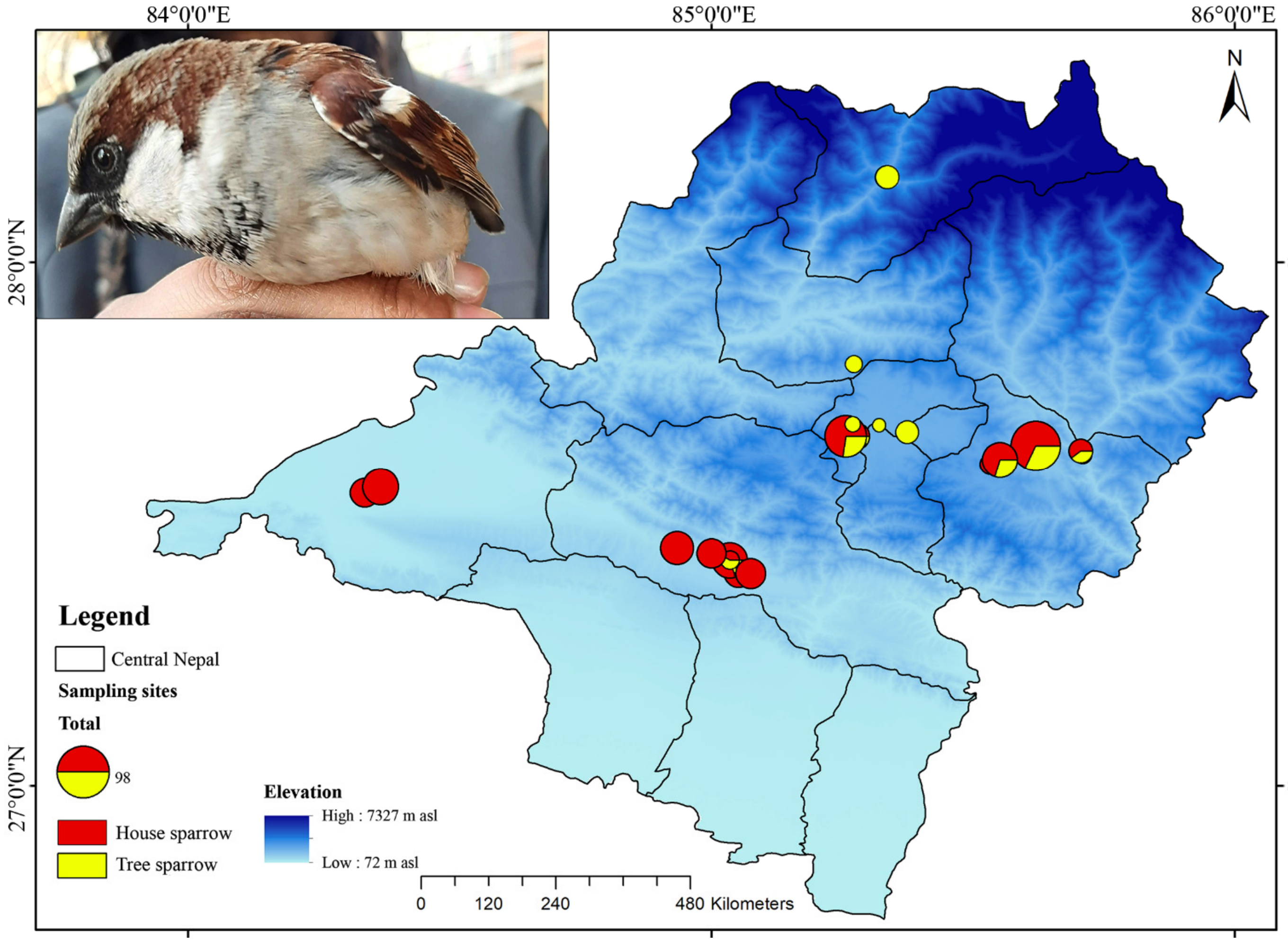

Figure 2. Map showing the distribution and sampling sites of *Passer domesticus* (red) and *P. montanus* (yellow) in central Nepal. The photo on the inset shows a *P. domesticus* from Dolalghat, Kavrepalanchok (688 m asl).

A total of 156 Eurasian tree sparrows were observed at 12 sites. The largest flock size observed consisted of 28 individuals from Dolalghat, Kavrepalanchok at 688 m asl and the smallest flock size was 6 individuals from Thapathali, Kathmandu at 1420 m asl. As noted above, gender determination could not be performed for Eurasian tree sparrows.

3.2. Inter-Species Morphological Variation

A total of 98 sparrows were captured and examined at all 22 survey points in central Nepal; this included 70 house sparrows (females = 39, males = 31) and 28 Eurasian tree sparrows. House sparrows had longer average tarsus, wing and bill lengths than the Eurasian tree sparrows (Figure 3). Conversely, the tail length and bill widths were greater in the Eurasian tree sparrow. All these differences were statistically significant, with the exception of bill width. Notably, the house sparrow had significantly higher body mass than the Eurasian tree sparrow (t = 4.139, df = 47, p <0.01).

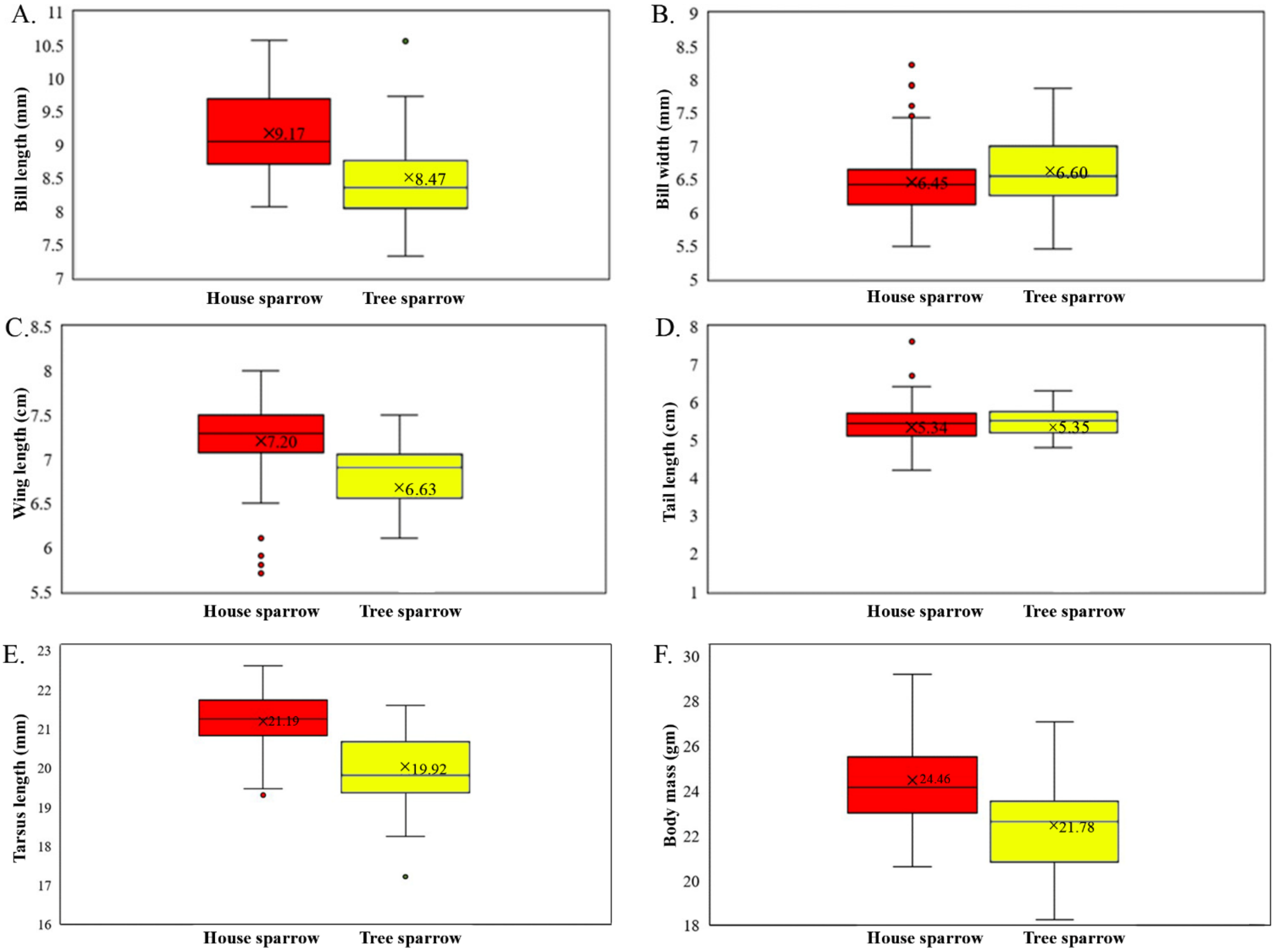

Figure 3. A comparative account of morphological measurements in *Passer domesticus* and *P. montanus:* (**A**). Bill length; (**B**). Bill width; (**C**). Wing length; (**D**). Tail length; (**E**). Tarsus length; and (**F**). Body mass. The lines and values inside the boxes indicate the medians and means, respectively.

3.3. Morphological Variations along the Elevational Gradient

In house sparrows, body mass, tarsus length, wing length and tail length increased significantly along the elevational gradient, whereas bill length decreased with elevation (Table 1, Figures 4 and 5), thus following both the Bergmann's rule and Allen's rule. Eurasian tree sparrows did not show any significant morphological variation along the elevational gradient (Table 1).

Table 1. Relationship between morphological measurements of sparrows and elevation.

Species	Parameter	Body Mass	Tarsus Length	Wing Length	Tail Length	Bill Length	Bill Width
P. domesticus	P	0.02	0.05	0.04	0.01	0.02	0.02
	r^2	0.08	0.06	0.06	0.09	0.08	0.14
P. montanus	P	0.88	0.96	0.26	0.96	0.88	0.16
	r^2	0.001	0.0001	0.05	0.0001	0.001	0.07

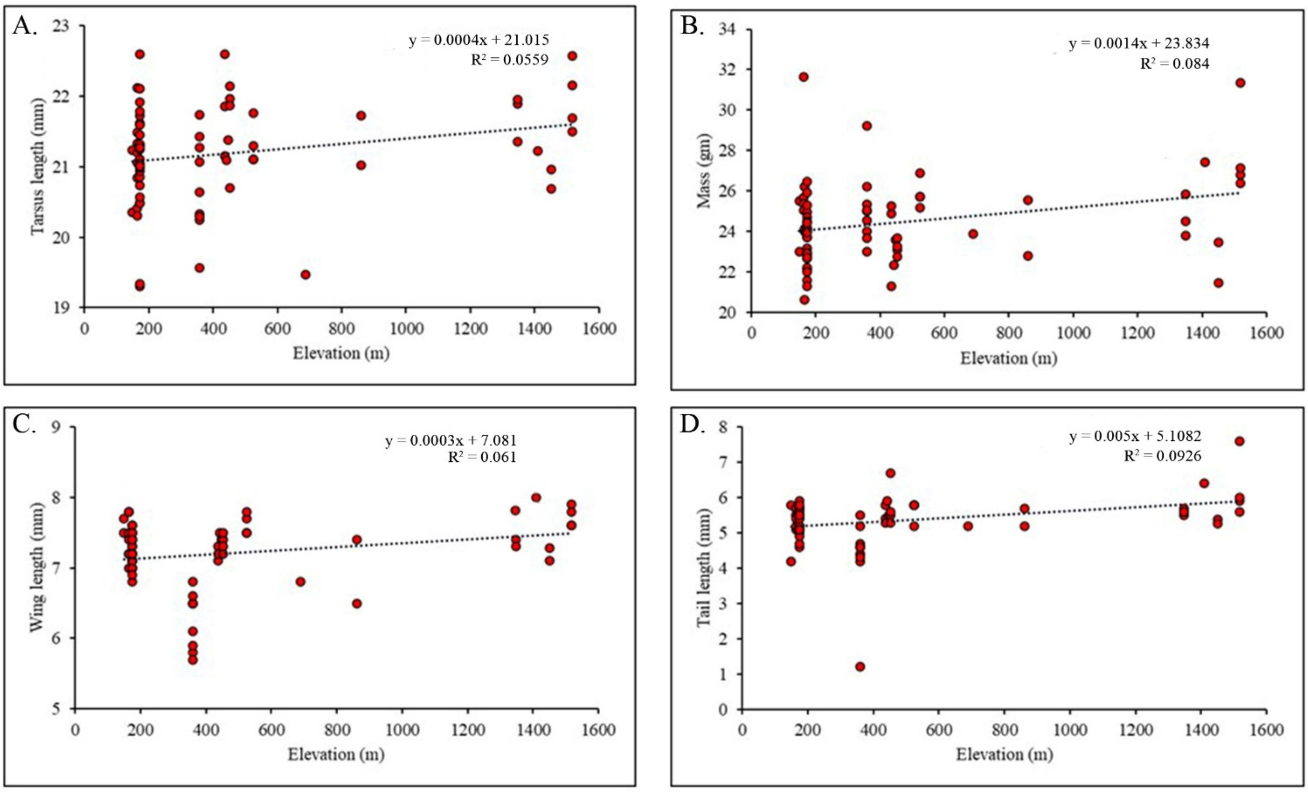

Figure 4. Morphological variations as a function of elevation in *Passer domesticus*. (**A**). Tarsus length vs. elevation; (**B**). Body mass vs. elevation; (**C**). Wing length vs. elevation; and (**D**). Tail length vs. elevation.

3.4. Association of Morphology with Climatic Variables

The body mass of house sparrow decreased significantly with annual precipitation (bio12, $r^2 = 0.144$, $p < 0.001$) and precipitation seasonality (bio15, $r^2 = 0.086$, $p < 0.01$). Wing length increased significantly with temperature seasonality, decreased with precipitation seasonality and precipitation of the coldest quarter (Table 2). Tail length decreased significantly with precipitation of the coldest quarter, whereas the bill width decreased significantly with annual precipitation.

Bill length was significantly associated with almost all bioclimatic variables except annual precipitation (bio12). It increased significantly with annual temperature (bio1), temperature seasonality (bio4), maximum temperature of warmest month (bio5), minimum temperature of coldest month (bio6), temperature annual range (bio7), mean temperature of warmest quarter (bio10), mean temperature of coldest quarter (bio11) and precipitation seasonality (bio15) (Table 2). It decreased significantly with precipitation of the warmest quarter (bio18, $r^2 = 0.229$, $p < 0.01$) and precipitation of the coldest quarter (bio19, $r^2 = 0.241$, $p < 0.01$).

The bill length of Eurasian tree sparrow significantly Increased with temperature annual range (bio7, $r^2 = 0.258$, $p < 0.01$) and significantly decreased with annual precipitation, precipitation seasonality and precipitation of the warmest quarter. Body mass increased significantly with the minimum temperature of the coldest month (bio6, $r^2 = 0.146$, $p < 0.05$). Unlike the house sparrow, the Eurasian tree sparrow showed no significant relation with the other bioclimatic factors.

Table 2. Relationship between morphological measurements of house sparrow and bioclimatic variables.

Traits	Parameter	Bio1	Bio4	Bio5	Bio6	Bio7	Bio10	Bio11	Bio12	Bio15	Bio18	Bio19
Body mass	*p*	ns	ns	ns	ns	ns	ns	ns	0.001 *	0.01 *	ns	ns
	r^2	ns							0.144	0.08		
Tarsus Length	*p*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	r^2	ns										
Wing length	*p*	ns	0.01 *	ns	ns	ns	ns	ns	ns	0.022 *	Ns	<0.01 *
	r^2	ns	0.08							0.075		0.19
Tail length	*p*	ns	ns	ns	ns	ns	ns	ns	ns	Ns	Ns	0.02 *
	r^2	ns										0.07
Bill length	*p*	<0.01 *	<0.01 *	<0.01 *	<0.01 *	<0.01 *	<0.01*	<0.01 *	ns	<0.01 *	<0.01 *	<0.01 *
	r^2	0.301	0.33	0.32	0.27	0.35	0.31	0.28		0.35	0.23	0.24
Bill width	*p*	ns	ns	ns	ns	ns	ns	ns	<0.01 *	ns	ns	ns
	r^2								0.15			

Notes: * = statistically significant; ns = not significant.

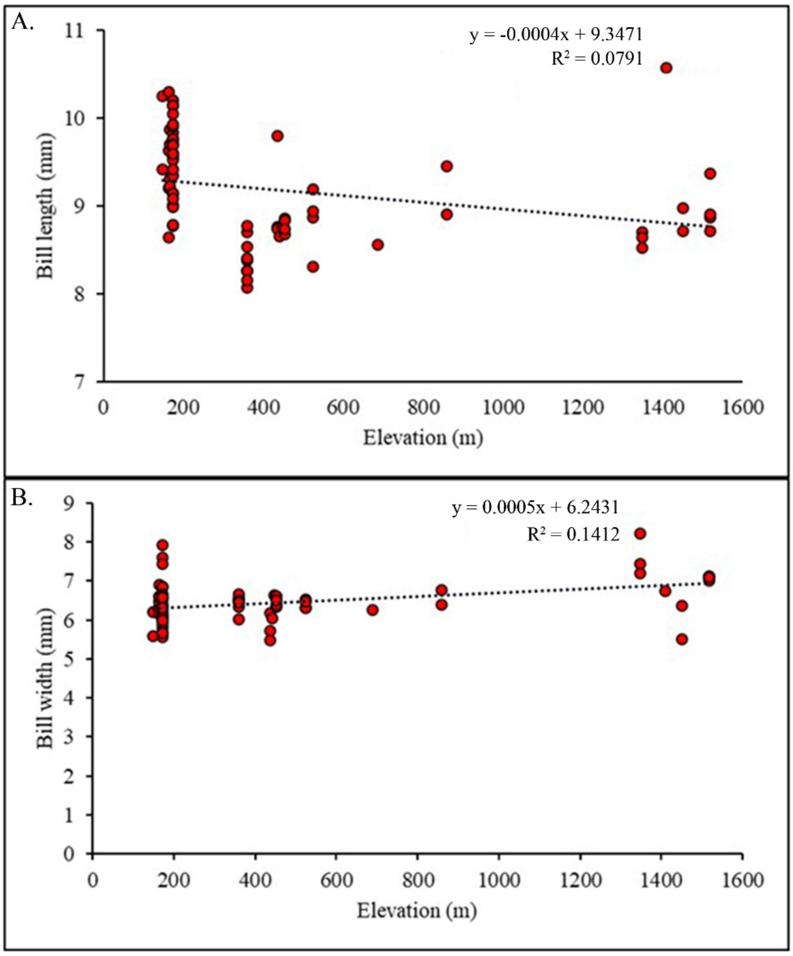

Figure 5. Bill length and width as a function of elevation in *Passer domesticus*. (**A**). Bill length vs. elevation, and (**B**). Bill width vs. elevation.

4. Discussion

Sparrows have a wide range of elevational distribution. Previous publications have reported house sparrows from 75 m to 2135 m asl and Eurasian tree sparrows from 75 m asl to 4270 m asl in Nepal [22]. In this study, house sparrows were observed from 149 m asl to 1518 m asl and Eurasian tree sparrows from 442 m asl to 1738 m asl. Additionally, studies have noted that Eurasian tree sparrows can live at higher elevations than house sparrows [32,33]. Similar findings were observed in this study with Eurasian tree sparrows found at higher elevations compared with house sparrows. This study also found significant variation in morphological measurements between the two species. House sparrows were bigger and heavier compared with the Eurasian tree sparrows in the central Himalayas. Similar results were observed in Spain [34] and Britain [32,35].

The house sparrow and Eurasian tree sparrow are sympatric species, originating from a common ancestor in the early Pleistocene [32]. They both share a similar ecological niche and have a similar appearance [32,34]. However, there are some key differences in nesting behavior and microhabitat selection between the two species [36]. Eurasian tree sparrows are mostly found in lightly wooded areas with trees, whereas house sparrows are found in towns, villages and farmlands [32]. Eurasian tree sparrows are more flexible when selecting nesting sites [37,38]. However, when there is an overlap of the ecological niche between the two species, competition is likely to occur. The house sparrow is typically dominant to the Eurasian tree sparrow since the former is more aggressive than the latter [32]. Although both the species are synanthropic and share a similar ecological niche, differences in microhabitat preference and nesting site selection are reflected in their morphological measurements.

The results of this study suggest that house sparrows followed both Bergmann's rule and Allen's rule. Body size such as mass, tarsus length, wing length and tail length were positively correlated with elevation, concordant with Bergmann's rule. Body appendages such as bill length decreased with increasing elevation in accordance with Allen's rule. Such a trend had been observed in several bird species, such as *Prunella modularis*, *Pyrrhula pyrrhula* [17], *Sylvia atricapilla* [39], *Melanerpes carolinus* [40], *Pycnonotus barbatus* [41] and *Passer domesticus* [42]. Increased body mass is the physiological response to a colder climate [2]. A larger-bodied individual means a reduced surface area to volume ratio which means they lose proportionately less heat compared with smaller bodied individuals [3,5,43]). Bills act as "thermal windows" from which heat is dissipated out of the body [44]. Smaller billed individuals are found in a colder climate [45] since this helps an individual retain heat, giving a similar effect as increased body size in a colder climate [14]. Temperature is related to elevation; it decreases with increasing elevation [46]. Hence, higher elevation favors individuals of the larger size as they can conserve heat, and lower elevation favors individuals of smaller size, as they can dissipate excess heat.

No significant variation in morphology along the elevational gradient was observed for Eurasian tree sparrows. In contrast to the findings of this study, Eurasian tree sparrows in mainland China followed Bergmann's rule [47]. Similar to the results of this study for Eurasian tree sparrow, several other bird species follow neither Bergmann's rule nor Allen's rule, e.g., *Cinclus cinclus* [16], *Suiriri suiriri* [18], *Galerida cristata*, *Acrocephalus scirpaceus* [17], *Erithacus rubecula* [39], and *Pica serica* [14]. Species might adopt different thermoregulation strategies to adapt to the environment [14]. The thickness of fur and feathers or changes in behavior help organisms to cope with environment gradient [48]. Temperature alone is not a good predictor of body size [49]. There might be some other driving forces in addition to temperature that determines the morphology of the species [45].

The wing length of house sparrow significantly increased with temperature seasonality. Seasonality increases body size because larger individuals can survive resource shortage periods due to the presence of their long-lasting energy reserves [50]. Bill length significantly increases with annual temperature, temperature seasonality, the maximum temperature of the warmest month, minimum temperature of the coldest month and temperature annual range. There is a strong correlation between elevation and temperature [51]. Average annual temperature on the Indian continent decreases by 0.5 °C with every 100 m rise in elevation [46]. Such a change in temperature along the elevational gradient affected the morphology of house sparrows. A larger bill length helps in the dissipation of a larger amount of heat to the environment [4]. Increased bill length of house sparrows with temperature variability confirms Allen's rule in the house sparrow.

In contrast to the expected pattern, the body mass of house sparrows decreased with annual precipitation and precipitation seasonality. The wing length decreased with precipitation seasonality and precipitation of the coldest quarter. The bill length of Eurasian tree sparrows decreased with annual precipitation, precipitation seasonality and precipitation of the warmest quarter. Bill width significantly decreases with annual precipitation. This may be because there is no distinct latitudinal precipitation pattern in Nepal due to the presence of topographical barriers (mountain ranges) [23]. In addition, there is no overall trend of precipitation in Nepal [52]. Due to the lack of a general pattern along the altitudinal gradient and specific trend of precipitation in Nepal, house sparrows also did not show any morphological pattern concerning precipitation. Therefore, it is concluded that Bergmann's rule and Allen's rule are not always valid but depend upon species-specific biological and ecological characteristics.

5. Conclusions

The house sparrows were found to be larger in body size compared with the tree sparrows. The body size of house sparrows increased, whereas bill size decreased along the elevational gradient, confirming to both Bergmann's and Allen's rule. The bill length of house sparrows showed significant association with almost all the bioclimatic variables used in the analysis and could be one of the best predictors for testing the Allen's rule. This study concludes that ecogeographical phenomena such as Bergmann's rule and Allen's rule could be species-specific based on their biological and ecological characteristics.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/ecologies3040034/s1, Figure S1: Matrix showing pairwise correlation coefficients among the six morphological measurements of sparrows from the elevational gradient of the Himalaya in central Nepal.

Author Contributions: Conceptualization, L.K. and A.G.; methodology, D.D.; software, D.D. and L.K.; validation, L.K., N.P. and R.C.K.; formal analysis, D.D. and N.P.; resources, L.K.; data curation, A.G; writing—original draft preparation, D.D.; writing—review and editing, L.K., N.P., R.C.K.; visualization, D.D.; supervision, L.K.; project administration, D.D.; funding acquisition, D.D. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: Data used in this study will be provided by the corresponding author upon genuine request.

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